TRANSMISSION OF VIBRATIONS ALONG PLANT STEMS: IMPLICATIONS FOR INSECT COMMUNICATION

Paul D. Bell

Abstract.—Many insects are known to communicate with percussive vibration and vibrations transduced with acoustic songs via plant tissue. Artificial percussive vibrations degrade in acceleration and velocity away from a vibration source along plant stems; the free end distorting and loosing energy faster than the fixed end. Woody stemmed plants vibrate within a narrow frequency band and thus transmit signals further than fleshy ones.

Nutritional imperatives, oviposition sites and predator avoidance constitute the major reasons many insects frequent certain species of plants. Nevertheless, another use of plants to insects may be to act as a communication channel. Representatives from many insect orders vibrate their plant substrate during mating and aggressive behavior (Table 1).

It is well documented that insects detect substrate vibrations with sensory neurons inervating the tympana and subgenual organs (Cokl et al. 1977; Fudalewicz-Niemezyk et al. 1978; Huber 1978; Kalmring et al. 1978).

Here are investigated the vibration transmission characteristics of various plants that tree crickets, *Oecanthus* spp. (Orthoptera: Gryllidae), are found on north of Huttonville, Ontario, Canada. The acceleration, velocity, wave form and duration of induced artificial vibrations that approximated *O. nigricornis* (Walker) percussive vibratory signals were measured from plants that tree crickets do and do not mate on. The transmission characteristics and vibrational physics of these plants below (fixed end) and above (free end) a vibrational source were determined.

Materials and Methods

An Exact 126 signal generator was set to deliver a 5 ms, 100 Hz sinusoidal pulse every 5 sec. A Marsland woofer converted these pulses into vibrations via a plastic probe. These signals as modified by the plant were measured with a Bruel and Kjaer 4344 accelerometer and a B.&K. 2304 impulse precision sound level meter for acceleration and velocity. The accelerometer and probe were mounted to the plant with a thin layer of bees' wax as outlined by Brock (1972). The vibrations were recorded with a Uher 4000 Report IC tape recorder and displayed on a Tektronix 455 oscilloscope (Fig. 1).

Ten each of orchard grass (*Dactylis glomerata* L.), raspberry canes (*Ru-*

Table 1.   Insects employing plant tissue to transduce vibratory signals.

Insect	Plant	Context	Reference
Orthoptera			
Neconema thalassinum	leaf ?	courtship	Ragge (1965)
Copiphora rhinocerous	stem ?	courtship	Morris (1980)
Neoconocephalus spp.	stem ?	courtship	Whitesell (1969)
Neoconocephalus ensiger	stem ?	aggression	Gwynne (1977)
Conocephalus nigropleurum	stem ?	aggression	Morris (1971)
Mogoplistinae	leaf, stem ?	courtship, post-copulation	Love & Walker (1978)
Oecanthus nigricornis	*Rubus* spp. etc.	courtship, post-copulation	Bell (1979a)
Oecanthus burmeisteri	sunflower leaf	calling	Prozesky-Schulze et al. (1975).
Plecoptera			
Perlidae etc.	*Phalaris* spp.	courtship, calling	Rupprecht (1968)
Hemiptera			
Oncopeltus fasciatus	*Asclepias* spp.	mating	Walker (1979)
Homoptera			
Dictophora europea	leaf ?	calling	Strubing (1977)
Euscelis incisus	leaf ?	calling	Traue (1978)
Coleoptera			
Golofa porteri	palm leaf, stalk aggression		Eberhard (1977)
Eusattus spp.	bark ?	?	Tschinkel & Doyen (1976)
Brentus anchorago	bark ?	?	Johnson, L. K. (pers. comm.)
Nothorrhina muricata	bark ?	courtship	Faber (1953)
Diptera			
Helius flavipes	*Pilea* spp.	male assemblages	Zalom (1979)
Euaresta spp.	*Ambrosia* spp.	calling	Batra (1979)
Liparia spp.	*Phragmites* spp.	calling	Mook & Bruggemann (1968)
Tephritis spp.	*Senecio* spp.	calling	Tauber & Toschi (1965)

bus spp.), Canada thistle stems (*Cirsium arvense* L.), common cattail leaves (*Typha latifolia* L.), toadflax (*Linaria vulgaris* Hill), and goldenrod (*Solidago* spp.) were individually tested for their vibration transmission characteristics. The parts of all plants ranged from 30–35 cm in height with a
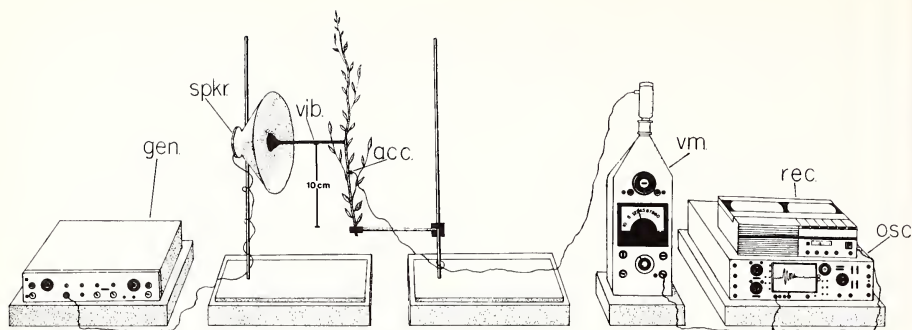
Fig. 1.   Vibration generation and reception apparatus. gen., signal generator; spkr., speaker; acc., accelerometer; vm., vibration meter; rec., tape recorder; osc., oscilloscope.

base diameter not varying by more than 0.5 mm within species. The accelerometer was affixed to each plant at 180° to the probe at 2.5, 5, 7.5, 10, 12.5, and 20 cm from the top of the plant base clamp. Canada thistle stems required shaving for probe and transducer attachment. The probe attached to each plant 10 cm above the base clamp (Fig. 1).

Results and Discussion

Intraspecific plant vibration transmission variation as indicated by the standard deviation for each of the sample groups of 10 was small. Variation was usually greater further away from the probe, especially above (20 cm above base) (Fig. 2).

Orchard grass, raspberry cane, Canada thistle and goldenrod had nearly flat vibration transmission curves; while cattail and toadflax had rapid signal decay with greater distortion away from the probe (Fig. 2, 3). Tree crickets have never been observed by the author to mate on the latter two species. Tree crickets mate on all others (Bell, unpublished data). Cattail and toadflax also displayed a 'whip' effect on either side of the probe, i.e., the intensity of the signal increased momentarily before diminishing. In all plants excepting raspberry cane the deterioration of the vibrations was faster at the distal end.

Generally the vibrations were more distorted above the probe. Orchard grass, goldenrod and to some extent raspberry cane had a wave form resembling a sine wave with a slow decay, that is a vibration which is slowly dissipating energy over a narrow frequency band, i.e., 'ringing.' This was especially evident 2.5 cm above the base, thereby allowing these stiff stemmed plants to transmit vibrations further with more energy than more flexible stalked plants (Fig. 3).

Substrate vibrational communication in insects has certain advantages over acoustic, chemical and visual modalities. Predators are known or ex-
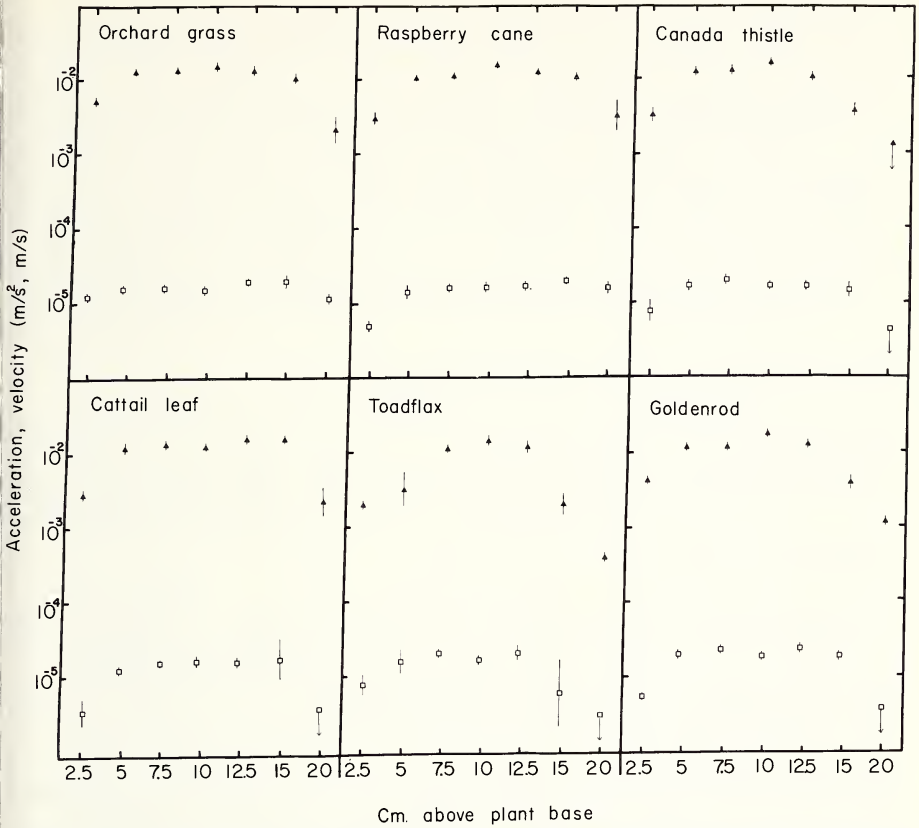
Fig. 2.   Acceleration (▲), and velocity (□) of artificial vibrations. Each point represents the mean value of 10 plant specimens; bars equal 1 standard deviation, arrows indicate levels below meter sensitivity.

pected to use acoustic cues to locate insect prey (Bell 1979b; Walker 1964; Rentz 1975). Certain parasites display positive phonotaxis to singing insects (Cade 1975; Soper et al. 1975). Thus it may be advantageous for some insects to reduce the occurrence of acoustic displays. However, selection against acoustic displays will eliminate some opportunities for mate attraction. Substrate vibration signals have the ability of signalling only conspecific females, while avoiding detection by predators and other males at longer distances (Morris 1980; Walker 1979). Acoustic signalling is attenuated, absorbed, refracted, reflected and diffracted by variations in foliage mass, height, species composition, humus layer, soil, and atmospheric conditions (Linskens et al. 1976; Martin and Marler 1977; Wiley and Richards 1978). In addition the airborne sounds of some insects are highly directional (Leroy 1976; Paul and Walker 1979).
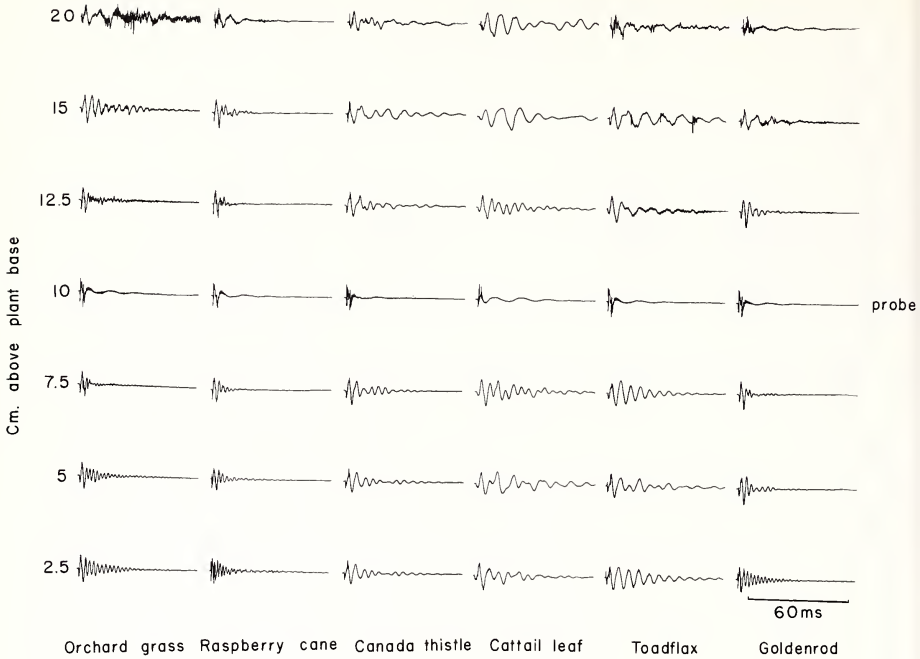
Fig. 3.   Oscillograms of plant transduced artificial vibrations.

Just as in acoustic signalling, the directionality of pheromones will limit mate attraction to those within the broadcast field. Olfactory signalling has been shown to function in close range communication, e.g. (Paul 1976), but would be ineffective in unfavorable air currents.

Visual signalling is limited in many nocturnal insects and hampered diurnally in some by dense vegetation (Bell 1979a).

Vibrations on the other hand proceed along plant tissue in front of and behind the signaller in a predictable manner. In the absence of interfering (in contact) foliage there is less potential degradation of vibrations over short (<1 m) distances than of visual and chemical signals. Traue (1978) reported that vibrations from leafhoppers were perceived 90 cm away through plant stems. A vibratotactic function for *O. nigricornis* percussive vibration signals has been indicated by preliminary experiments. Also, the temporal integrity of the male tree cricket calling song is preserved as substrate transduced vibrations through the insects legs, and may assist orienting females (Bell, in progress).

The present study has demonstrated that the quality of vibration signals is dependent on the species of plant involved in transduction. Tree crickets and many other insects may exploit the vibration transmitting characteristics

of plants to signal conspecific mates. It is likely that as plants age, develop new structure, and succumb to changes in turgor pressure, they begin or cease to have vibrational characteristics that are advantageous for insect signalling. Selection would favor insects which could successfully select a substrate that could transmit their messages over greater distances without distortion and degradation. These individuals would increase their likelihood of attracting potential mates only. It is probable that certain plants such as orchard grass and raspberry cane are frequented by tree crickets because of their high 'Q' resonance qualities, which allow vibrational energy to be released over a narrow frequency band, thereby travelling further.

Acknowledgments

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Department of Zoology, Erindale College, University of Toronto, Mississauga, Ontario, L5L 1C6 Canada.